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Genomics meets applied ecology:

Characterizing habitat quality for sloths in a tropical agro-ecosystem

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Abstract

Understanding how habitat quality in heterogeneous landscapes governs the distribution and fitness of individuals is a fundamental aspect of ecology. While mean individual fitness is

generally considered a key to assessing habitat quality, a comprehensive understanding of habitat quality in heterogeneous landscapes requires estimates of dispersal rates among habitat types. The increasing accessibility of genomic approaches, combined with field-based demographic methods, provides novel opportunities for incorporating dispersal estimation into assessments of habitat quality. In this study, we integrated genomic kinship approaches with field-based estimates of fitness components and Approximate Bayesian Computation (ABC) procedures to estimate habitat-specific dispersal rates and characterize habitat quality in two-toed sloths (*Choloepus hoffmanni*) occurring in a Costa Rican agricultural ecosystem. Field-based observations indicated that birth and survival rates were similar in a sparsely-shaded cacao farm and adjacent cattle pasture-forest mosaic. Sloth density was threefold higher in pasture compared to cacao, whereas home range size and overlap were greater in cacao compared to pasture. Dispersal rates were similar between the two habitats, as estimated using ABC procedures applied to the spatial distribution of pairs of related individuals identified using 3,431 SNP and 11 microsatellite locus genotypes. Our results indicate that crops produced under a sparse overstory can, in some cases, constitute lower quality habitat than pasture-forest mosaics for sloths, perhaps because of differences in food resources or predator communities. Finally, our study demonstrates that integrating field-based demographic approaches with genomic methods can provide a powerful means for characterizing habitat quality for animal populations occurring in heterogeneous landscapes.

Introduction

Characterizing habitat quality for species occurring in heterogeneous landscapes is a key endeavor of ecology, where high-quality habitats are expected to lead to high mean individual fitness in the absence of density dependent effects (Johnson 2007). Theoretically, individuals will seek to promote their fitness by preferentially selecting high- over low-quality habitats

(Orians 1969, Franklin *et al*. 2000, Morris 2003), and estimating mean individual fitness in different habitat types is therefore considered the "gold standard" for assessing habitat quality (Johnson 2007). Fitness, however, is also a function of the density of conspecifics within a habitat patch as intraspecific competition for resources can modulate the fitness benefits of high-quality habitats (Hassell & May 1973, Milinski 1979). Consequently, individuals must balance perceived tradeoffs between habitat quality and intraspecific competition when selecting habitat in order to maximize their contribution to future generations. The ideal free distribution (IFD) predicts that freely dispersing and omniscient individuals will preferentially select high-quality habitats until density reaches a level where intraspecific competition equalizes mean fitness between high and low-quality habitats (Fretwell & Lucas 1970, Fretwell 1972). Individuals are then expected to distribute themselves such that densities are greater in high- than low-quality patches. In contrast, the ideal despotic distribution (IDD) predicts patterns in distribution when competitively dominant individuals possess high-quality habitats (Fretwell 1972). Under the IDD, individual fitness is expected to be greater in high- than low-quality habitats because intraspecific competition limits density in high-quality habitats (Calsbeek & Sinervo 2002).

Habitat quality and habitat selection models, however, cannot be fully characterized or tested in heterogeneous landscapes without an understanding of how individuals move among habitats. When conspecifics do not exclude each other from high-quality habitats (i.e., do follow an IFD model), dispersal is expected to be "balanced", with high- and low-quality habitats exchanging equal numbers of dispersers such that per-capita rates of dispersal are biased in the direction of high-quality habitat (McPeek & Holt 1992, Tattersall *et al*. 2004). In contrast, when dominant individuals exclude subordinate conspecifics from high-quality habitats, individuals are expected to disperse from higher-quality "source" to lower-quality "sink" habitats (Pulliam 1988, Morris 2003). Thus, characterizing habitat quality within a

spatial context hinges on estimating the magnitude and directionality of per-capita dispersal rates among habitats, in conjunction with an understanding of the species' social system (Pulliam 1988, Armstrong 2005).

Given the importance of understanding dispersal movements among habitats in ecology, a myriad of methods to estimate dispersal rates have been developed. These approaches have been developed under the auspices of two sub-disciplines that are distinct in both philosophy and technology. Despite a host of advances, estimating dispersal rates remain challenging for many natural populations under either of these paradigms. Indeed, telemetry and mark-recapture techniques can be difficult to implement over sufficiently broad spatial and temporal scales (Kendall & Nichols 2004), whereas traditional population genetic methods require simple demographic assumptions and yield estimates that apply to long time scales (Pearse & Crandall 2004, Palsbøll *et al*. 2010, Palsbøll *et al*. 2013). Genetic assignment methods reflect recent time periods and apply to non-equilibrium populations, but perform poorly when dispersal rates are high (Wilson & Rannala 2003, Waples & Gaggiotti 2006, Hall *et al*. 2009). Moreover, while the rapidly evolving field of landscape genetics has provided novel insights into the environmental factors that impede or facilitate dispersal movements, distinguishing between historical and recent processes, as well as estimating per-capita dispersal rates, remains challenging (Palsbøll *et al*. 2010, Epps & Keyghobadi 2015, Samarasin *et al*. 2016).

The aforementioned limitations have stimulated the development of kinship-based approaches that integrate methods traditionally associated with either molecular or population ecology to estimate recent dispersal rates when movements are sufficiently frequent to apply more classical approaches with reasonable precision (Palsbøll 1999, Peery *et al*. 2008, Palsbøll *et al*. 2010, Wang 2014). In the simplest sense, a recent dispersal event can be inferred when the two close relatives (identified from their multi-locus genotypes) are

sampled in different localities. Inference applies to a time scale equivalent to the number of overlapping generations and is not hindered by genetic homogeneity resulting from frequent dispersal, as is the case for more classical population genetic approaches including assignment tests (Palsbøll *et al*. 2010). In addition, kinship-based methods are well-suited for species with high dispersal rates given that frequent movements facilitate the sampling of dyads in two different populations, and individuals need only be identified or sampled on a single occasion.

Despite their promise, kinship methods for estimating recent dispersal rates have, until recently, been hindered by the absence of a formal analytical framework for translating the spatial distribution of related individuals into estimates of per-capita dispersal rates. Peery *et al*. (2008) developed an individual-based population modeling approach for calculating the expected distribution of the number of related dyads in a single population (or habitat) under different rates of immigration, expectations that can then be compared to observed patterns of relatedness and used to infer immigration rates. More recently, Wang (2014) developed an Approximate Bayesian Computation (ABC) approach that allows for the estimation of dispersal rates between pairs of populations (or habitats) from genetic kinship data by comparing observed patterns of relatedness to expectations derived from populations in a more formal analytical framework. This approach is appealing as ABC methods, like full Bayesian procedures, allow for the explicit treatment of uncertainty in parameter estimates (e.g., reproductive and survival rates) via the specification of prior probabilities, but do not require the evaluation of full likelihoods which is difficult and often computationally infeasible for complex models (Beaumont *et al*. 2002, Beaumont 2010, Csilléry *et al*. 2010). Nevertheless, estimates of dispersal rates from kinship approaches must be combined with habitat-specific estimates of fitness components such as reproduction and survival to fully

characterize the quality of different habitat types within heterogeneously distributed landscapes.

Inferences from kinship methods also have the potential to be strengthened by taking advantage of the increasing accessibility of genomic approaches made possible by the advent and refinement of high-throughput sequencing technologies. Approaches relying on microsatellite markers typically characterize the spatial distribution of related individuals based only on parent-offspring dyads because they can be identified with high confidence using microsatellite markers and "exclusion" methods (Palsbøll 1999, Peery *et al*. 2008, Wang 2014). Discriminating other types of relations (even full-siblings) is impractical with typical numbers of loci (Weir *et al*. 2006, Skaug *et al*. 2010, Woltmann *et al*. 2012), yet ignoring lower-order relationships greatly reduces the data upon which dispersal rates are inferred. The development of high-throughput sequencing technologies now provides the means to genotype thousands of, for example, single nucleotide polymorphism (SNP) loci in large samples of individuals (Lerner and Fleischer 2010, Davey *et al*. 2011), thereby enabling the identification of dyads of lower-order relatives with confidence (Skare *et al*. 2009). In concert, the emergence of ABC estimation techniques and genomic approaches for identifying lower-order relationships has opened up new, although hitherto unexplored, frontiers for understanding dispersal processes and habitat quality in heterogeneous landscapes (Holderegger & Wagner 2008, Allendorf *et al*. 2010, Kool *et al*. 2013).

Here, we integrated "genomic" kinship approaches, field-based estimates of fitness components, and ABC procedures to estimate habitat-specific dispersal rates and characterize habitat quality for two-toed sloths (*Choloepus hoffmanni*) occurring in a Costa Rican agricultural ecosystem. Assessing the potential benefits that agro-ecosystems can provide to arboreal and forest-associated species such as tree sloths is considered a key to conserving tropical biodiversity (Sala *et al*. 2000, Faria *et al*. 2007, Abrahamczyk *et al*. 2008), and

understanding the quality of different habitats within agro-ecosystems is fundamental to this objective. Our study area was defined by two adjacent habitats: a shade-grown cacao plantation ("cacao") with a sparse over-story of native and non-native trees and cattle pastures-forest mosaic ("pasture") containing buffers of tropical forest in riparian areas and isolated legacy trees (Fig. 1). We did not compare sloth fitness or estimate sloth dispersal rates between "pure pasture" habitat and forest habitat because it was not possible to definitively assign individuals to one or the other habitat given that individual sloths frequently used both pastures and the narrow riparian forests that intersected this habitat type. Previous radio-telemetry work indicates that individual two-toed sloths generally maintain long-term home ranges within either of these habitats (Peery & Pauli 2012, Mendoza *et al*. 2015). We also tested for differences in space use characteristics such as home range size and overlap (from telemetry information) between the two habitats given that social structure can modulate individual dispersal movements (Calsbeek & Sinervo 2002, Ridley & Sutherland 2004). In addition to demonstrating how the integration of genomic and field-based demographic approaches can provide a powerful means for estimating dispersal, our results indicate that a pasture with remnant forest may provide higher-quality habitat than shade-grown crops for some arboreal, tropical species using agricultural ecosystems.

Methods

Study site and fieldwork

Our study area was located 85 km northeast of San José, Costa Rica where the shade-grown cacao plantation consisting of native and non-native trees was surrounded by banana and pineapple monoculture to the east and west, human development, grassland with narrow (~20 m) tropical forest riparian strips to the south and pastures with tropical forest riparian strips and isolated trees to the north (Fig. 1). We captured sloths by hand from trees from February

2010 to December 2013. We marked each captured individual with a uniquely coded PIT tag (Biomark, Boise, ID, USA) inserted subcutaneously between the shoulder blades and collected tissue for genetic analysis in the form of an ear punch using sterilized sampling instruments. We determined sex by examining external genitalia and estimated the body mass to the nearest 0.1 kg using a digital scale. We classified individuals into one of three life stages (early sub-adult, late sub-adult, or adult) based on body mass and behavioral observations similar to Peery & Pauli (2012) in order to parameterize the population model at the core of the ABC estimation procedure. Young sloths were characterized as early sub-adults when they were no longer carried by their mother and began using nearby branches. Individuals who had been early sub-adults for at least one year with a body mass below the criterion form adults were classified as late sub-adults. Males and females were classified as adults if their body mass was >4.5 kg and >4.8 kg, respectively, based on minimum body masses observed in reproductive individuals. We affixed VHF radio collars to a subsample of individuals of all age classes for relocation purposes and survival estimation. Individuals that did not receive a radio collar were marked with a uniquely identifiable neck collar. A more detailed description of the study area and capture methods were described by Peery & Pauli (2012). Sloth captures and handling were conducted as stipulated and authorized by IACUC protocol A01424 issued by the University of Wisconsin-Madison and by the Ministerio del Ambiente y Energía de Costa Rica, Sistema Nacional de Áreas de Conservación de Costa Rica, Área de Conservación La Amistad Caribe (ACLAC), Dirección Regional Área de Conservación, permit SINAC-ACLAC-PIME-R-041-2015.

Characterizing local demography

We assessed female reproductive status using visual observations of radio- and color-marked adult females following the methodology established by Peery & Pauli (2012). Females bear and rear young throughout the year. Females provide maternal care for a single juvenile for several months following parturition, and juveniles are readily observed clinging to their mothers (Taube *et al*. 2001). We considered an adult female to have reproduced successfully in a given year if she was observed with a juvenile. We considered an adult female not to have bred in a given year if she was not observed caring for a juvenile at least once in each of the four annual quarters (i.e., 3-month periods) and was observed in ≥6 months that year (Peery & Pauli 2014). Females that failed to meet the minimum criterial for determining breeding status were considered to be of unknown reproductive status for that year. We tested for differences in annual birth rates between the two habitats (and years) using logistic regression models implemented in SAS 9.4 (SAS Institute Inc., Cary, NC, USA) where the breeding status (1 = yes, 0 = no) was employed as the response variable. We estimated annual birth rates under three different models: (i) constant, regardless of habitat type or year; (ii) habitat-specific; and (iii) year-specific, and ranked models with AIC. Because the maximum possible ΔAIC is 2 when an uninformative parameter is added, we considered the habitat- and year-specific models to be poorly supported if they did not have lower AIC values than the constant model (Arnold 2010).

We estimated annual survival rates using mortality observations of radio-collared sloths. We estimated survival rates for two stage classes: (i) early sub-adults and (ii) late sub-adults and adults pooled (hereafter we refer to this pooled estimate as "adult survival" for convenience). Early sub-adult sloths were radio-collared at the approximate time of independence from their mothers and monitored from March 2013 to May 2014. Late sub-adult and adult sloths were radio-collared and monitored from February 2010 to April 2014.

We generally located all radio-collared animals several times per month and recorded their locations and whether they were alive or dead. Thus, we were able to assign which habitat type an animal was using each month, including at the time of death. We used known-fates models (Pollock *et al*. 1989) implemented in program MARK (White & Burnham 1999) to estimate monthly survival rates. We raised monthly survival rates to the 12^{th} power to obtain annual survival rates ($\hat{S}$) and calculated sampling variance using the delta method (Seber 1982, Oehlert 1992). We estimated a single survival rate for early sub-adults regardless of sex or habitat type because only ten individuals in this stage class were radio-collared. For late sub-adult and adult sloths, we estimated survival rates under three different models: (i) constant, regardless of habitat type or sex; (ii) habitat-specific; and (iii) sex-specific, and ranked models with AIC. As noted above for birth rates, we considered the habitat- and sex-specific survival models to be poorly supported if they did not have lower AIC values than the constant model (Arnold 2010).

We estimated habitat-specific densities based on the number of unique sub-adult and adult individuals we captured and marked in each habitat during 2013. We assumed that sloth surveys achieved a near-complete census of the two age classes within the boundaries of the two habitats in 2013 (Fig. 1). Indeed, we captured only 8 and 16 unmarked adults in 2012 and 2013, respectively (all of which were subsequently marked and included in density estimates), compared to 73, and 34 new adults marked in 2010 and 2011, respectively. This high percentage of animals accounted for in our study contrasts other sloth work in which finding even radio-tracked individuals in the canopy is extremely difficult. Point estimates of density were then calculated by dividing the number of marked sloths in 2013 by the area of the habitat present in our study area (Fig. 1). Area was based on total geographic area of the site. Although calculating area of only suitable habitat for sloths (i.e. trees) would be a more

conservative estimate of suitable habitat area, due to the isolated trees and patchiness of tropical forest in the pasture we chose total geographic area of the site.

Home range size and overlap

We estimated the 90% home range size for the 15 adult females and 25 adult males from which we collected a minimum of 50 radio-telemetry locations using fixed kernel methods. Relocation points were collected at minimum two to five days apart therefore eliminating issues of temporal autocorrelation. Home ranges were delineated using ESRI's ArcGIS 10.1 (ESRI 2011) and adehabitatHR package (Calenge 2006) for R with href as the smoothing parameter. For each individual's home range, we also tallied the number of conspecifics with overlapping home ranges. We then performed a two-way ANOVA in R 3.0.1 (R Core Team 2013) using sex and habitat as independent variables to test for differences in mean home range size and number over overlapping home ranges.

Genotyping

We genotyped the sampled sloths using both SNP and microsatellite markers to increase confidence in pairwise relatedness assignments. Individuals were genotyped at 11 unlinked microsatellite loci developed specifically for Hoffmann's two-toed sloths (Moss *et al*. 2011) using methods described in Peery & Pauli (2012). Individuals were genotyped at SNP loci using double-digest Restriction Associated DNA (ddRAD) sequencing (Peterson *et al*. 2012). A detailed description of the laboratory procedures and data analysis used to develop SNP genotypes is provided in Fountain *et al*. (2016); here, we provide an overview of these methods. Genomic DNA was extracted using a Qiagen DNeasy™ Blood and Tissue Kit

(Qiagen Inc., catalog #59506) following the manufacturer's protocol for tissue. We digested tissue samples using the restriction endo-nucleases *Eco*RI (HF) and *Msp*I (New England BioLabs Inc., MA, USA) and cleaned digests with Agencourt AMPure™ XP beads (Beckman Coulter Genomics Inc., Danvers, MA). Samples were quantified using a Qubit®2.0 Fluorometer (Invitrogen Inc., Carlsbad, CA, USA) and split into three groups based on concentration (low, medium, and high). We standardized the concentrations of the digested genomic DNA within each group and ligated the DNA to P1 adapters that bind to *Eco*RI-created restriction sites and contained a unique 5 base pair (bp) barcode, and P2 adapters binding to overhangs generated by *Msp*I. After ligation, we pooled samples with unique barcodes and size-selected using a 2.5% agarose dye-free cassette with internal standards on Pippin Prep™ (Sage Science Inc., Beverly, MA, USA) for 550-595bp. Samples were split between four libraries based on the DNA concentration after restriction enzyme digestion. Each library contained a total of 38 individuals, and was pair-end sequenced to 101bp with the Illumina HiSeq2000 in two lanes, which contained a single PhiX control lane at University of Wisconsin-Madison Biotechnology Center, USA.

Demultiplexing, sequence data processing, and genotype calling were conducted in Stacks 1.24 (Catchen *et al*. 2013). Raw sequence reads were demultiplexed by barcode and index and trimmed to 90bp to remove low-quality base pairs. The remaining sequences were pair-end aligned to the *C. hoffmanni* reference genome version 1.0 (GCA_000164785.1) using SOAP2 (Li *et al*. 2009). We retained only the SNPs genotyped with a minor allele frequency ≥ 0.02, a coverage ≥ 15 and that were shared with at least 60% of individuals. Individual with less than 40% of their genotypes below a coverage ≥ 15 were not considered in dispersal analyses. We tested for deviations from Hardy-Weinberg Equilibrium (HWE) and calculated Weir and Cockerham's F_{ST} (Weir & Cockerham 1984) for both marker types in Genepop 4.0 (Rousset 2008). For F_{ST}, we combined the SNP and microsatellite markers;

however, due to computational limitations the number of SNPs was reduced to 1989 most polymorphic loci. To reduce the potential effects of linkage disequilibrium among SNPs on dispersal analyses, we retained a single (the most polymorphic) SNP per genome scaffold.

ABC estimation of dispersal rates

We used ABC approaches to estimate annual per-capita dispersal rates between cacao and pasture based on patterns of relatedness, derived from the SNP and microsatellite data, within and among habitats. As is the case with the approach developed by Wang (2014), our implementation involved comparing estimates of relatedness-based summary statistics for genotyped sloths to the same set of summary statistics derived from simulations of an individual-based, two-patch population model parameterized with a range of values for survival, growth, birth, and dispersal rates. However, unlike Wang (2014), our underlying population model provided a means to account for overlapping generations (see below), as is the case in sloths. A model validation using simulated populations with known (and sloth-like) demographic characteristics indicated that our approach can yield reasonably precise and unbiased estimates of dispersal rates with sample sizes of individuals and loci similar to those employed in this study (Supplementary Material 1).

At the center of our ABC approach was a population model that projected groups of individuals in the two habitat types (cacao and pasture) forward in time according to stage-specific birth and survival rates, as well as habitat-specific dispersal rates (i.e., prior probabilities). The population model was structured based on the following three stages: early sub-adult (0-year old), late sub-adult (1- and 2-year olds), and adult (≥3 year olds). In each population simulation, stage-specific, population-level birth and survival rates were randomly drawn from normal distributions with means and standard deviations equal to estimates

derived from field studies (see below for estimates). Habitat-specific dispersal rates were randomly drawn from a uniform prior distribution ranging from 0 to 0.5. The initial numbers of individuals in each habitat type were also drawn from a uniform distribution ranging from 50 to 1,000 individuals. Simulated populations were projected forward in time for 56 years (approximately 7 sloth generations), by which time relatedness summary statistics had stabilized. Population growth over this period was regulated according to the Beverton-Holt model of density dependence on survival rates (Beverton & Holt 1957) to prevent simulated populations from going extinct or becoming unrealistically large. Multi-locus SNP and microsatellite genotypes in the first year of population simulations were randomly assigned to individuals based upon the observed allele frequencies in our study population. In subsequent years, multi-locus genotypes were generated for offspring following the rules of Mendelian inheritance in absence of novel mutations. In each generation, we assumed a 1% genotyping error rate and assigned errors to genotypes randomly. Finally, we assumed a random mating system given frequent observations of promiscuous mating behaviors and mate-switching in female two-toed sloths (Peery & Pauli 2012, Garces-Restrepo, *in review*).

At the end of each 56-year population simulation, 104 individuals (corresponding to the number of sloths we sampled and genotyped) were randomly sampled from the population and relatedness summary statistics were calculated from their genotypes. The likelihood of a dyad being related parent and offspring or second-degree-relatives was estimated from multi-locus genotypes and the most likely relationship was treated as the true relationship (see Supplementary Material 2 for details; Broman & Weber 1998, Epstein *et al*. 2000). We then tallied the number of dyads related as parent and offspring or second-degree-relative dyads where both members were sampled in the same or different habitat (either cacao or pasture) in the same and different years. We did not consider dyads related as full-

siblings since full-sibling dyads can be more susceptible to incorrect assignments resulting from genotyping errors than second-order dyads such a half siblings (Kopps *et al*. 2015).

Using an ABC-SMC (Sequential Monte Carlo) algorithm (Sisson *et al*. 2007) with four SMC populations, we collected 2,000 realizations for the posterior distributions. Each estimation consisted of five initial iterations with a 1% tolerance level, which was used to seed the remainder simulations that were conducted using a 0.1% tolerance level. We conducted three separate ABC estimation runs following the above-described procedures to evaluate the convergence of the dispersal rate estimates. All ABC analyses were conducted on the University of Groningen Peregrine High Performance Computing cluster.

To visualize and quantify how closely related individuals were distributed within and among habitats, we estimated the pedigree of the sampled individuals using the software FRANz 2.0.0 (Riester *et al*. 2009). We adopted this approach because: (i) the above methods did not provide a statistical test of alternative relationships for computational ease; and (ii) other kinship software could not accommodate the large number of loci used in this study. We employed the genotypes collected from the 3,431 SNPs and 11 microsatellites loci from all 104 sloth samples employed in the above in the ABC analysis. We used known parent-offspring relationship (based on behavioral observations), sex of the individuals, and assigned a younger age to sub-adults as priors. We set the maximum number of candidate fathers at 110 (*Nmmax* parameter in FRANz) and the maximum number of candidate mothers at 150 (*Nfmax* parameter in FRANz) based on our sloth capture data, and we set genotyping error to 0.01 based on previous assessments of the error rate reported by Fountain *et al.* (2016). In order to increase the number of parent-offspring dyads, we conducted a second parentage

analysis for 102 additional sloths that were only genotyped at the 11 microsatellites. We used the pedigree from the previous SNP parentage analysis as a prior. We did not identify full siblings with the microsatellite-only analysis as, based on simulations, discerning full-sibling relationships accurately from parent and offspring dyads can require ≥40 microsatellites (Kopps *et al*. 2015).

Results

Local demography

We used reproductive outcomes for 64 adult females on 146 occasions from 2011-2013 to estimate annual birth rates. The intercept-only model (i.e., no habitat or sex effects) was the most supported by reproductive data. Based on this model, we estimated the probability that a female bred during a given year to be 0.67 (SE = 0.04). Little support existed for models in which the birth rate differed by habitat type (ΔAIC = 0.68) or year (ΔAIC = 2.48). Based on the model where birth rate varied by habitat type, females using pasture (0.69, SE = 0.05) had slightly higher birth rates than those in cacao farms (0.62; SE = 0.08; Fig. 2A), although the habitat effect was not statistically significant ($X_1^2 = 1.33$, P = 0.25).

We obtained 1,762 monthly encounters for the 68 radio-marked late subadult and adult sloths, no individuals went missing and we observed 11 mortalities among these individuals during the tracking period. The cause of mortalities were predation by feral and domestic dogs (*n* = 4), predation by jaguar (*n = 1*), electrocution (*n* = 2) and unknown (*n* = 4). The intercept-only model (i.e., no habitat or sex effects) was the most supported by the known-fates data. Based on this model, we estimated that annual survival was 0.928 (SE = 0.021) for late subadults and adults. Little support existed for models with annual survival differing by habitat type (ΔAIC = 1.995) or sex (ΔAIC = 1.987). Annual survival was similar

between cacao ($\hat{S}$ = 0.930, SE = 0.034) and pasture ($\hat{S}$ = 0.926, SE = 0.027; Fig. 2B) based on the model where survival differed by habitat type. We obtained 117 monthly encounters for the 10 sloths radio-marked as early subadults, and observed a single mortality among these individuals over the tracking period. We estimated that annual survival for young subadults was 0.902 (SE = 0.093) with these data.

We captured and marked a total of 122 adult and sub-adult sloths within study area boundaries delineated to estimate habitat-specific densities (Fig. 1), excluding three individuals that used both cacao and pasture habitats. We assigned 35 and 87 sloths to cacao and pasture, respectively, leading to density estimates of 0.27 and 0.67 sloths/ha for the two habitat types (Fig. 2C).

Home range size and overlap

Mean home range size was greater in cacao than pasture ($F_{1, 36}$ = 17.24, P < 0.001) and for males than females ($F_{1, 36}$ = 4.64, P = 0.04; Fig. 2D). The mean number of intersecting home ranges for sloths was greater in cacao than pasture ($F_{1, 36}$ = 5.64, P = 0.02; Fig. 2E), but did not differ significantly by sex. We did not detect a significant interaction between habitat and sex for either home range size or the number of intersecting home ranges ($F_{1, 36}$ = 0.79, P = 0.38 and $F_{1, 36}$ = 0.28, P = 0.60, respectively).

Genetic data

We called 4,962 SNP loci in the 114 sloths sampled for genetic analyses. A total of 104 individuals were included in the ABC-based estimation of dispersal rates; ten sloths were excluded from this analysis because a coverage of ≥ 15 was achieved at less than 40% of loci.

Of the 4,962 loci, 478 deviated from HWE and 1,053 occurred on the same genome scaffold and were thus considered linked. After removing loci that departed from HWE expectations or retaining one locus from those that were putatively linked, 3,431 loci were included in the ABC analysis. The percent of missing data at an allele on average was 22% in the remaining SNPs across the 104 sloths. The mean minor allele frequency was 0.146, and mean expected and observed heterozygosity were 0.205 and 0.207, respectively. Pairwise F_{ST} for sloths occurring in cacao and pasture estimated using the 11 microsatellites and 1989 most polymorphic SNP loci was 0.006.

Mean observed and expected heterozygosity at the 11 microsatellite loci was 0.62 (range: 0.36 – 0.78) and 0.63 (range: 0.38 and 0.80), respectively (Supplementary Table S1). The mean number of alleles was 6 and the number of loci ranged from 3 – 8. No microsatellite locus deviated from HWE expectations (all *P*'s > 0.05).

ABC estimation of dispersal rates

Posterior distributions were similar among the three independent ABC runs (Fig. 3), and inferences regarding point estimates and credible intervals were therefore drawn from their combined distribution. The dispersal rate from cacao to pasture (mode = 0.030; median = 0.084, 95% HPD: 0.001 to 0.322) was similar to the dispersal rate from pasture to cacao (mode = 0.032, median = 0.064, 95% HPD: 0.001 to 0.265). While there was considerable uncertainty in point estimates of dispersal, the central tendency in and shape of the posteriors distribution was highly concordant between habitat types. Both distributions were positively skewed with longer right than left tails, presumably because estimates were left truncated at zero, with very low probabilities with high dispersal rates (Fig. 3).

Based on our FRANz analysis, 13 parent-offspring dyads were identified in the SNP pedigree and an additional 12 dyads were identified in the microsatellite pedigree (the latter of which included a greater fraction of the sloths in our study area). Most parent-offspring dyads co-occurred in the same habitat type, with 56% of dyads occurring in cacao, 36% of dyads occurring in pasture, and only 8% of dyads split between habitats (Table 1, Fig. 4). We detected 11 full-sibling dyads with 37% of dyads occurring in cacao, 37% of dyads occurring in pasture, and 27% of dyads split between habitats (Table 1, Fig. 4). The inferred directionality of dispersal (based on ages) in the two instances where parent-offspring were split between habitats was from pasture to cacao (Fig. 4).

Discussion

Characterizing habitat quality for species occurring in heterogeneous landscapes is a fundamental, yet challenging, endeavor in ecology. For two-toed sloths, the degree of genetic divergence estimated between the two habitat types (cacao and pasture) was, unsurprisingly, very low (F_{ST} = 0.006), a level where individual genetic assignment approaches performs poorly (Waples & Gaggiotti 2006, Hall *et al*. 2009, Gaggiotti & Foll 2010). Presumed permanent movements by individuals between the two habitats were detected only on three occasions, by individuals that were not radio-marked (and only observed incidentally), precluding the estimation of dispersal using telemetry or mark-recapture approaches. This dual issue – low genetic structure yet infrequent dispersal movements - is likely common in species where groups of individuals use different habitats in close proximity to one another and thus complicates the characterization of dispersal patterns and assessments of habitat quality in general. Notably, kinship approaches provided the ability to detect dyads of close relatives split between different habitats (Fig. 4, Table 1), which were indicative of dispersal movements, using samples taken during a relatively short period of time. Moreover, by

integrating genomic-based kinship and field-based demographic information in an ABC framework, we were able to estimate habitat-specific dispersal rates for two-toed sloths which in turn yielded novel insights into the quality of two habitat types commonly present in tropical agro-ecosystems for an arboreal mammal species.

Mean birth and survival rates for sloths using cacao and pasture were similar, suggesting that, on average, realized fitness did not differ appreciably between habitats - despite markedly different vegetation composition and structure (Fig. 1). However, sloth density was almost threefold higher in the pasture-forest mosaic than cacao. Although density is not always an indicator of habitat quality (van Horne 1983, Hall *et al*. 1997, Bock & Jones 2004), the greater density in the pastures-forest mosaic and similar realized fitness between the two habitats suggest density is indeed a good indicator of habitat quality for sloths in our study. The high densities in pastures may depress birth and survival rates via density dependent effects such that fitness in the two habitat types was effectively equal, consistent with an IFD model. Thus, on a per-capita basis, habitat quality was similar, but pastures were able to support greater numbers of sloths per unit area suggesting a higher quality on a population level. Our conclusion that the pasture was of a higher quality compared to the cacao was supported by smaller home ranges and less home range overlap in the former than latter habitat type. Indeed, when food resources are relatively scarce, individual organisms tend to range over larger areas and are less likely to defend space from conspecifics (Maher & Lott 2000, Mcloughlin *et al*. 2000). Alternatively, our study area is depauperate in two important predators of sloths, jaguars (*Panthera onca*) and harpy eagles (*Harpia harpyja*), and the absence of these predators may contribute to sloth high densities in pastures, particularly in open areas outside of riparian forests.

Nearly symmetrical dispersal between the two habitats, as estimated from the distribution of related individuals, conflicted with the expectation that dispersal would be greater into high-quality habitats under an IFD. However, several reasons could exist for symmetric dispersal rates by sloths in a landscape containing habitats of different quality. First, two-toed sloths exhibit complex patterns of space use that may modulate how individuals are able to disperse between habitats to establish new breeding areas. Some male sloths share large parts of their home ranges with other males, whereas other males maintain exclusive core areas, sharing only peripheral areas of their homes ranges with other males (Peery & Pauli 2012). Thus, some degree of territorial exclusion may have impeded dispersal into pasture and led to patterns of dispersal inconsistent with an IFD. Second, dispersal may have been mediated by inbreeding avoidance, where a greater proportion of sloths may have dispersed from low- (cacao) to high- (pasture) habitat than expected under an IFD to avoid mating with relatives. Third, IFD models assume that individuals have perfect knowledge of habitat quality. Sloths with their limited mobility may not be able to assess this landscape-scale heterogeneity in habitat quality to the extent needed to optimize the fitness benefits of dispersal. Regardless, low dispersal rates (~0.03 sloths/year) were consistent with our previous studies indicating that adult sloths maintain long-term home ranges and sub-adults often remaining adjacent to their parents for several years before dispersing to establish their own breeding territories (Peery & Pauli 2012, Pauli & Peery 2012).

The population model underlying our ABC estimation approach did not account for immigration into our study area from unsampled surrounding areas. We were unable to assess the effect of this omission as we did not radio-collar individuals outside of the study area and quantify immigration rates. However, we note that the study area was bordered by unsuitable and likely impermeable habitat (monocultures) to the south, east, and west such that any

immigration likely only occurred from one direction. Moreover, immigration from such unsampled "ghost populations" tends to result in right-skewed posterior distributions for dispersal rates. Nonetheless, small immigration flow, as observed in this study, has little impact on measures of central tendency such as the median because it is unlikely that small immigration flow greatly affects the number of sampled kinship dyads in the sampled habitats (Kang *unpubl. data*). Thus, we concluded that immigration was not likely to result in a great degree of bias in the dispersal rate estimates or affect our conclusion that dispersal was modest and similar between the two habitats.

Our study not only provides a novel approach for characterizing habitat quality and dispersal in a heterogeneous landscape but has several implications for the conservation of tropical biodiversity. Agricultural ecosystems, and particularly shade-grown crops, are increasingly pointed to as a tool for conserving tropical biodiversity while also meeting the demand for agriculture (Perfecto *et al*. 1996, Rice and Greenberg 2000, Sala *et al*. 2000, Faria *et al*. 2007, Abrahamczyk *et al*. 2008). Indeed, arthropod, mammalian, avian, and plant biodiversity are generally higher in shade-grown farms compared to adjacent monocultures, and can harbor a significant proportion of the biodiversity encountered in surrounding, intact forests (Greenberg *et al*. 1997; Harvey *et al*. 2006; Faria *et al*. 2007; Abrahamczyk *et al*. 2008; Cicuzza *et al*. 2011). However, it is less clear to what extent shade-grown agricultural systems provide a suitable habitat for arboreal obligates, such as sloths, that are perceived as most likely to be impacted by the conversion of tropical forest (Peery & Pauli 2014), particularly given that species diversity is often lower in shade-grown systems than in adjacent patches of intact forests (Perfecto *et al*. 2003, Faria *et al*. 2007).

Our study was unique in regards to the demographic information obtained on a tropical species, not just in an agricultural ecosystem, but in two types of habitats that are becoming increasingly common in modified tropical landscapes. The observation that highly converted pasturelands containing thin buffers of riparian forests constitute higher-quality habitat for two-toed sloths than the shade-grown cacao plantation supports previous work that the fraction of the original biodiversity remaining within shade-grown agro-ecosystems typically depends on the density, species composition, and diversity of the overstory trees retained within the planted area (Rice & Greenberg 2000, Clough *et al*. 2009). As the overstory present in the cacao plantation was sparse and contained non-native trees not consumed by sloths such as *Eucalyptus* (Mendoza *et al*. 2015), it was perhaps unsurprising that the cacao habitat type was of relatively low quality for sloths. Nevertheless, while sloth densities were relatively low, the cacao planation appeared to support a viable population of two-toed sloths, which suggests that even sparsely shaded plantations provide better habitat than intense agricultural production types such as sun-grown plantations or pastures without suitable trees. However, our study focused on a single species occurring in a single small study area, and that this system may not be representative of the wide range of modified landscapes and agro-ecosystems present in the Neotropics.

We regularly observed females rearing young in isolated - and even non-native - trees in the pasture, indicating that pasture can provide suitable habitat for two-toed sloths when they contain trees necessary for foraging and resting. However, previous selectivity analyses in the two-toed sloth showed that individual sloths preferentially use riparian forest over pure pasture at our study site (Mendoza *et al*. 2015). Moreover, sloth densities were twofold higher in the riparian forest (1.10 sloths/ha) than pastures (0.56 sloths/ha) in our study using a criterion where 75% of an individual's telemetry locations had to occur in forest or pasture

for a habitat assignment to be made. A greater density of sloths spending most of their time in the riparian forests suggests that the inferred high quality of the pasture habitat relative to the cacao habitat can be, to a degree, attributed to the presence of riparian forests in pastures. Thus, these results support previous studies demonstrating the importance of riparian forest buffers to tropical species in modified landscapes (Laurance & Laurance 1999, Gillies & St. Clair 2008, Ibarra-Macias *et al.* 2011, Kormann *et al.* 2016). Furthermore, using the criterion described above, density within pasture (excluding riparian forest) was greater than density in cacao (0.27 sloths/ha), suggesting that the isolated trees in the pasture may provide adequate habitat for sloths. Given that biodiversity within shade-grown agricultural systems appears to be positively associated with the prevalence of intact forests in the surrounding area, we suspect that retaining patches of forest within agro-ecosystems is likely key to maintaining tropical species beyond sloths within such landscapes.

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Author contributions

EDF generated genomic data and conducted genomic, dispersal and homerange analyses; JK created ABC program to obtain dispersal estimates, DJT conducted field-based reproduction and survival analyses; JNP, PJP and MZP designed the study. All authors contributed to the text and approved the final manuscript.

Data accessibility

Genomic and ecological data associated with this article is deposited on Dryad, doi:10.5061/dryad.3278c.

Supporting Information

Additional supporting information may be found in the online version of this article.

Supplementary Material 1. Validation of ABC model to estimate dispersal rates in sloths.

Supplementary Material 2. Relationship category calculations in the ABC model.

Table S1. Polymorphism detected at 11 microsatellites in 104 Hoffmann's two-toed sloths.

Table 1. Number of first-order dyads with both pair members within cacao, with both members within pasture, and where the members were split between the two habitat types.

	Cacao	Pasture	Split
Parent offspring	14	9	2
Full sibling	4	4	3
Total 1st order dyads	18	13	5

Figure 1. Map of study area in northeastern Costa Rica. Black line indicates study area boundaries used for density estimation. The original capture location for individuals used in the dispersal estimation is marked by black dots. Individuals outside the study are boundaries had recapture points within the study area and were therefore included in dispersal analyses.

Figure 2. Habitat-specific estimates of birth rates (A), annual survival rates (B), density (C), home range size (D), and number of intersecting home ranges for an individual (E). Error bars in (A) and (B) represent standard errors. Boxplots in D and E represent median, 25th and 75th percentiles, with whiskers extending to a maximum of 1.5 x IQR.

Figure 3. Posterior distributions for annual dispersal rates for sloths in cacao and pasture habitats, as estimated using ABC methods applied to the distribution of related pairs of individuals derived from SNP and microsatellite data. The three analysis replications are indicated by the different shaded bars. The dispersal rates between pasture and cacao are similar with the highest frequency at 0.05.

Figure 4. Parent-offspring (PO) and full-sibling (FS) dyads inferred using FRANz that were split between cacao and pasture habitat. The arrows indicate the probable direction of dispersal inferred from the relative ages of individuals in parent-offspring dyads.

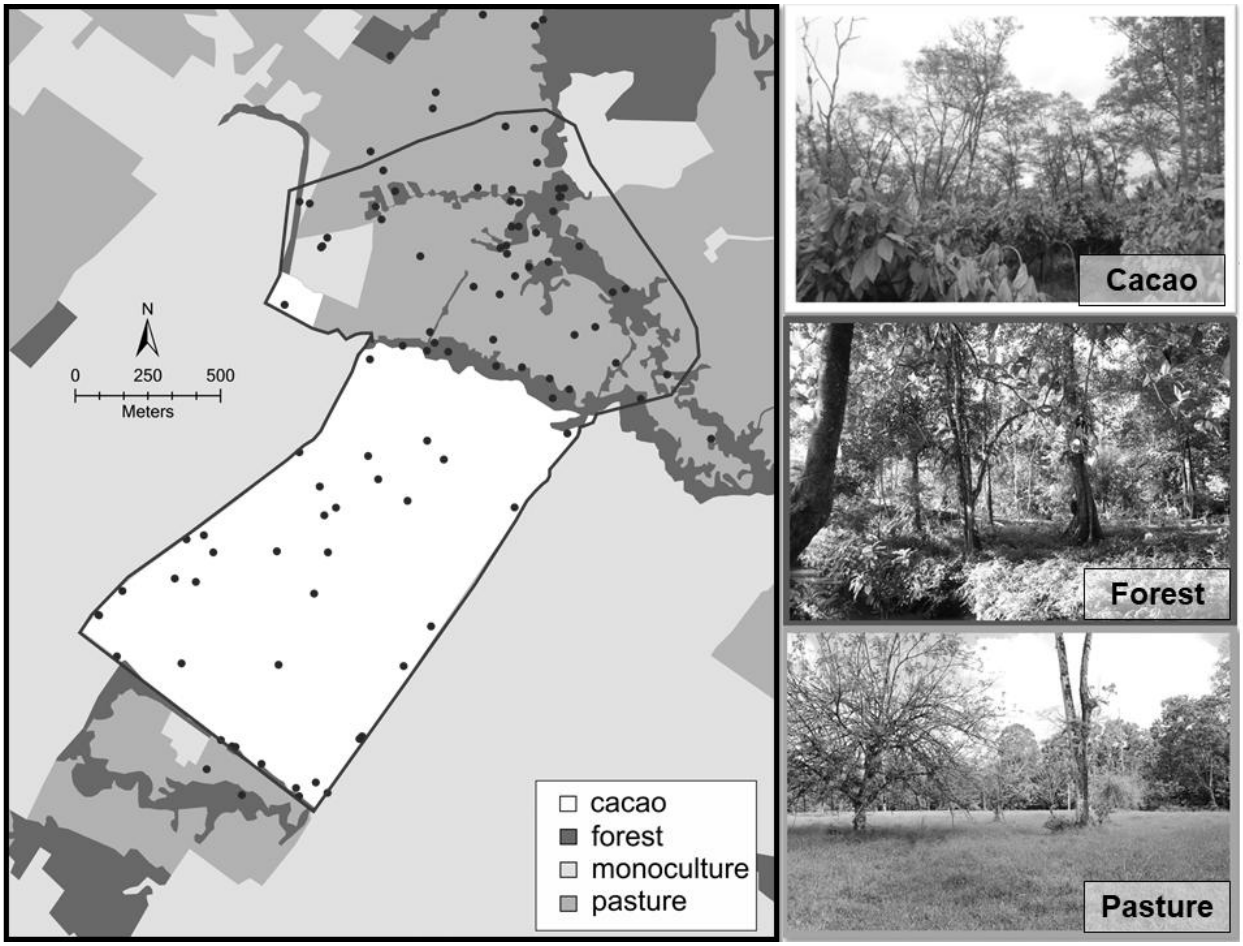
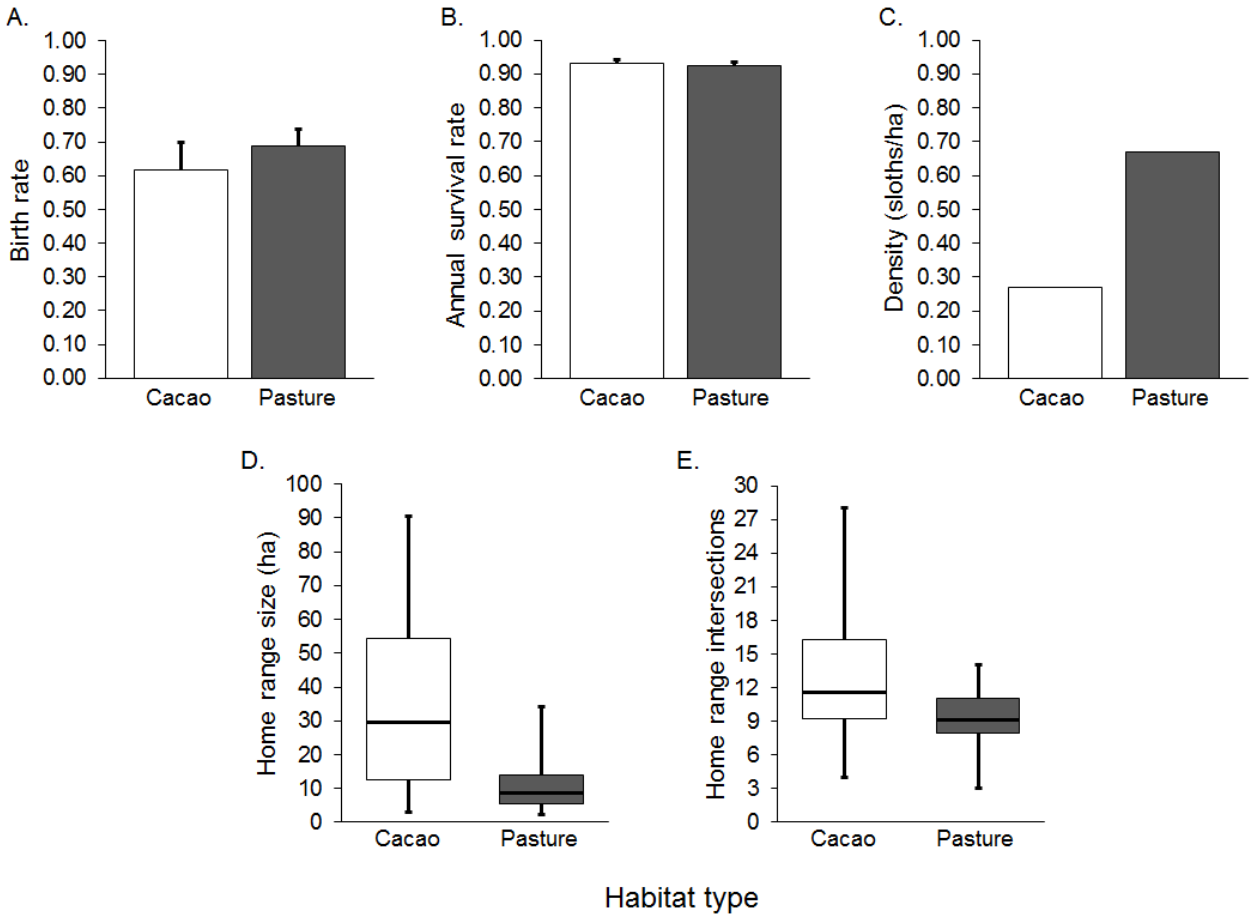


Figure 1.



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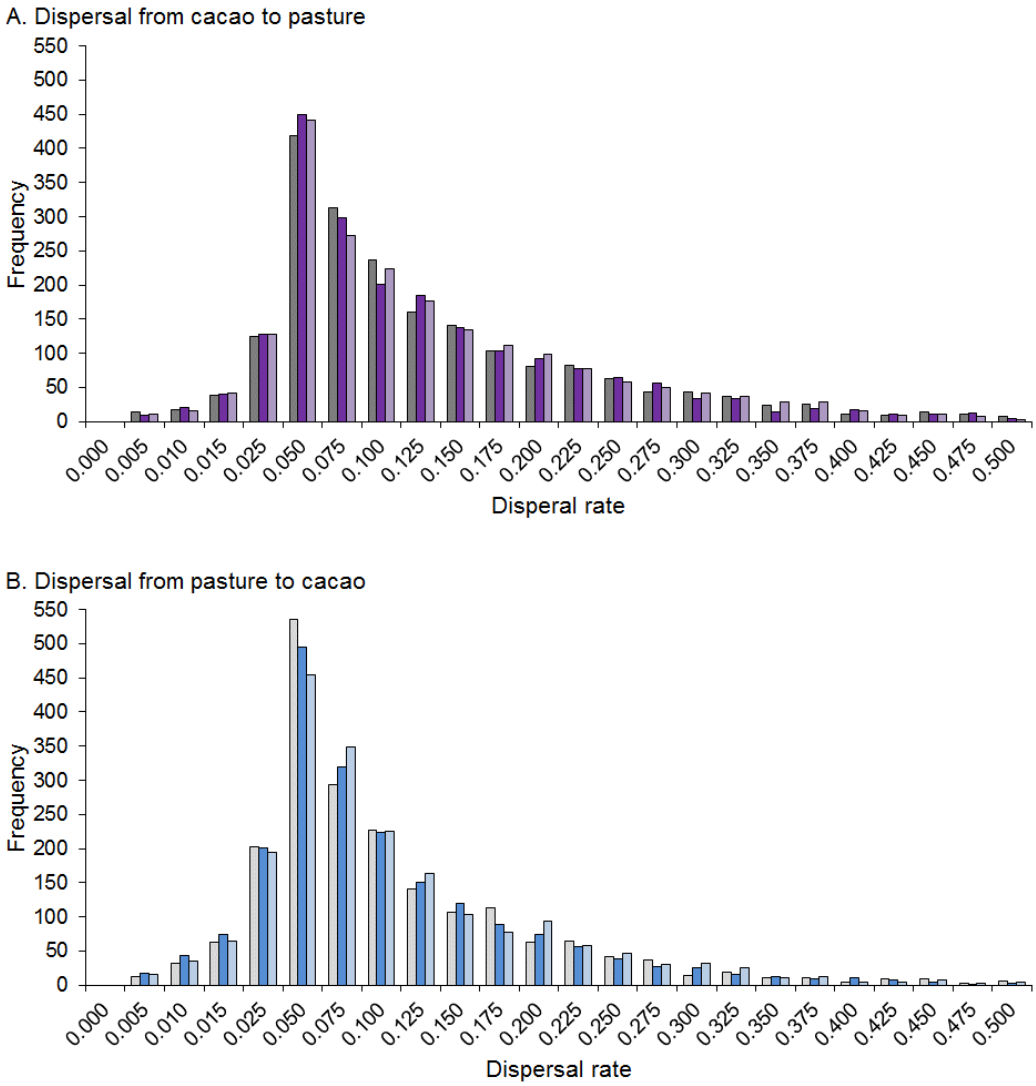

Figure 3.

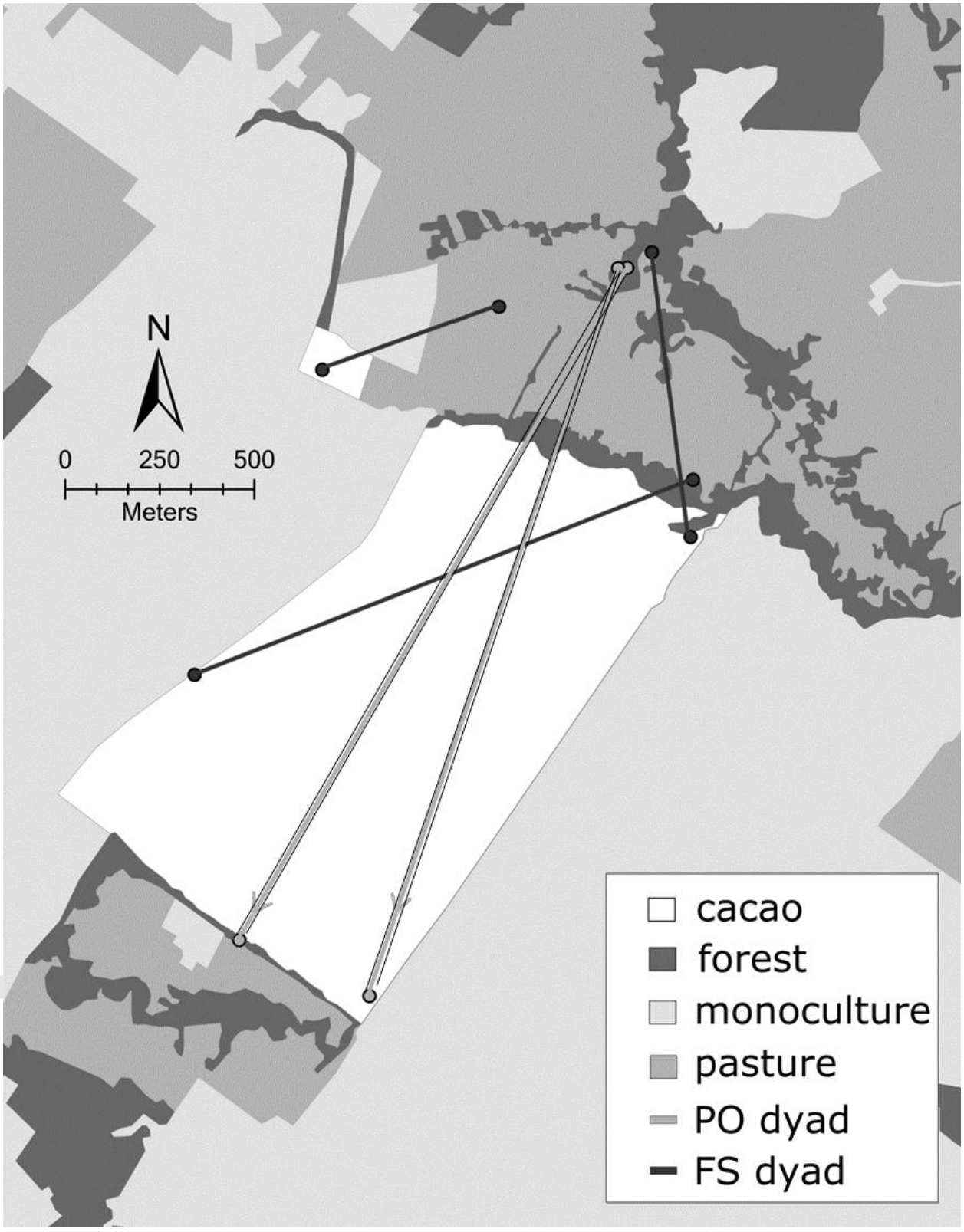

Figure 4.